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KAIROMONAL RESPONSE BY FOUR *Monochamus* SPECIES (COLEOPTERA: CERAMBYCIDAE) TO BARK BEETLE PHEROMONES

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Abstract—We investigated the hypothesis that wood-boring beetles in the genus *Monochamus* (Cerambycidae) utilize pheromones of sympatric bark beetles as host-finding kairomones. All nine bark beetle pheromones tested electrophysiologically were antenally active for both sexes of *M. scutellatus*, *M. clamator*, and *M. obtusus* from British Columbia. When field-tested with multiple-funnel traps (British Columbia) or cross-vane traps (Ontario), a blend composed of frontalin, ipsdienol, ipsenol, and MCH, in combination with a blend of host volatiles attracted significant numbers of *M. clamator, M. obtusus, M. notatus,* and *M. scutellatus* to baited traps. Traps baited with host volatiles in combination with a second blend composed of *endo*-brevicomin, *exo*-brevicomin, *cis*-verbenol, *trans*-verbenol, and verbenone caught no more beetles than unbaited traps or traps baited with the host blend alone. In British Columbia, traps baited with the first blend alone or both blends together captured more *M. scutellatus* and *M. clamator* than unbaited traps, demonstrating a response to bark beetle pheromones in the absence of host volatiles. These results suggest that *Monochamus* spp. are minimizing foraging costs by using the pheromones of sympatric bark beetles as kairomones.

Key Words—Coleoptera, Scolytidae, Cerambycidae, Buprestidae, *Monochamus*, chemical ecology, allelochemics, kairomones, coevolution.

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INTRODUCTION

Most wood-boring insects reproduce in stressed, dying, or dead trees that are usually randomly distributed in space and time (Schroeder, 1992). The larvae feed under the bark in the phloem tissue, in the sapwood, and sometimes deep into the heartwood (Linsley, 1961), often boring long tunnels that weaken and degrade the wood and provide infection courts for wood-rotting fungi. Wood-boring beetles have caused economic losses as high as 30% in British Columbia log yards (Safranyik and Raske, 1970). A southern interior British Columbia mill, which converts 700,000 m^3 of coniferous timber into lumber annually, could expect annual degrade losses from all wood-borers to total US $1.8–4.8 million (Phero Tech Inc. 7572 Progress Way, RR#5, Delta, British Columbia. V4G 1E9, Canada. Damage Assessment of Woodborers in the Interior of British Columbia. Unpublished report. 1997). If these values were extrapolated to encompass all interior mills, annual losses would be US $293 million, $43.6 million of which would be attributable to large wood-borers. Wood-borers in the genus *Monochamus* are of particular economic significance, because in addition to causing significant physical damage (Parmelee, 1941; Gardiner, 1957, 1975), they are vectors of the pinewood nematode, *Bursaphelenchus xylophilus* (Vallentgoed, 1991).

Coniferophagous wood-borers use olfactory stimuli to locate hosts (Linsley, 1961), and many are attracted to host monoterpenes and ethanol (Chénier and Philogène, 1989). Consequently, commercial wood-borer baits consist of host monoterpenes (usually α-pinene) and ethanol to simulate the odor of a stressed or dying tree. Current understanding of the cues involved in host selection by wood-borers is incomplete.

There is considerable overlap in pheromone components among sympatric scolytid beetles (Borden, 1982), facilitating kairomonal responses by entomophagous insects to trees or logs infested by bark beetles of numerous species (Vité and Williamson, 1970; Dixon and Payne, 1979; Bedard et al., 1980; Bakke and Kvamme, 1981; Raffa and Klepzig, 1989). The association between bark beetles and wood-boring beetles has long been recognized but has only been formally tested twice (Billings and Cameron, 1984; Billings, 1985). A kairomonal response to bark beetle pheromones would be adaptive to host-seeking wood-boring beetles because it could aid them in locating suitable host material. Coniferophagous wood-borers in the families Cerambycidae and Buprestidae often attack the same hosts at the same time as conifer-infesting bark beetles (Dahlsten and Stephen, 1974; Stephen and Dahlsten, 1976; Dixon and Payne, 1979; Coulson et al., 1976, 1980).

Subcortical interactions between bark beetles and wood-boring beetles have been classified as competitive (Coulson et al., 1976, 1980; Schroeder and Weslein, 1994a,b) or commensal (Flamm et al., 1989). A decline in larval density or emergence of adult bark beetles was attributed primarily to competition between

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cerambycid and bark beetle larvae. A kairomonal response to bark beetle pheromones would be even more adaptive to host-seeking wood-borers if bark beetle larvae represent a food resource for wood-borer larvae. Dodds et al. (2001) found that 74% of the six-spined ips, *Ips calligraphus*, larvae encountered by *Monochamus carolinensis* larvae in phloem sandwiches were attacked; 85% were killed, suggesting that cerambycid larvae may be facultative predators of bark beetle larvae. This result supports the earlier observation by Schenk and Benjamin (1969) that in Wisconsin "up to 50% of a brood in the egg and 1st instar was destroyed by cerambycid larvae; a single cerambycid larvae could reduce the available food supply by 3%." However, Flamm et al. (1989) found that foraging by *M. titillator* results in low mortality of the southern pine beetle *Dendroctonus frontalis*, because the larvae migrate to the outer bark before *M. titillator* foraging becomes significant. One possible explanation for the observed behavior is coevolution between *M. titillator* and *D. frontalis*, with larval *D. frontalis* migration to the outer bark being an adaptive response that would reduce mortality due to *M. titillator* predation.

Billings and Cameron (1984) and Billings (1985) found a kairomonal response by the southern pine sawyer, *Monochamus titillator*, to a blend of *Ips* spp. pheromones (ipsenol, ipsdienol, and *cis*-verbenol). In one study, there was a synergistic interaction between this stimulus and blends of *endo*-brevicomin and verbenone, or *endo*- plus *exo*-brevicomin with verbenone, all of which are pheromones of *D. frontalis* (Billings and Cameron, 1984). In the other study, this stimulus was synergized by loblolly pine, *Pinus taeda*, turpentine (Billings, 1985). Raffa (1991) reported an undisclosed number of *M. carolinensis* captured in ipsdienol-baited traps. Miller and Borden (1990) captured *Monochamus clamator* in increasing numbers as the combined release rates of ipsdienol and (−)-β-phellandrene increased.

There is considerable potential in exploiting bark beetle pheromones in wood-borer management, if they prove to be attractive to pest species. We report the results of experiments in British Columbia and Ontario demonstrating that certain bark beetle pheromones are attractive to *M. clamator*, *M. obtusus*, the white-spotted sawyer *Monochamus scutellatus*, and the northeastern sawyer *M. notatus*.

METHODS AND MATERIALS

Adult *M. clamator*, *M. scutellatus*, and *M. obtusus* were collected on emergence from caged bolts of lodgepole pine, *Pinus contorta* var. *latifolia*, and ponderosa pine, *P. ponderosa*. Coupled gas chromatographic–electroantennographic detection (GC-EAD) analyses were performed on the antennae of both male and female *M. clamator*, *M. scutellatus*, and *M. obtusus* with an HP 5890 gas chromatograph equipped with a fused silica column (DB-5, 30 m × 0.32 mm ID,

J&W Scientific, Folsom, California 95630-4714) (Gries, 1995). Authentic samples of nine candidate bark beetle pheromones (ipsenol, ipsdienol, MCH, frontalin, *cis*-verbenol, *trans*-verbenol, *exo*-brevicomin, *endo*-brevicomin, and verbenone) (Borden, 1985) were mixed in hexane solutions at concentrations of both 10 ng/μl and 100 ng/μl. These were analysed in 1-μl amounts by GC-EAD under splitless conditions with a temperature program of 60°C (1 min) then 10°C/min to 220°C. The analyses were repeated with a temperature program of 50°C for (1 min), then 10°C/min to 90°C and 4°C/min to 240°C to separate ispdienol and *trans*-verbenol.

Synthetic antennally active pheromones were arbitrarily partitioned into two blends: blend 1 consisting of ipsenol, ipsdienol, MCH, and frontalin and blend 2 consisting of *cis*- and *trans*-verbenol, *exo*- and *endo*-brevicomin, and verbenone (Table 1). These were tested in the field for behavioral activity with and without a host blend composed of ethanol and α-pinene (experiment 1) or ethanol with a synthetic host blend (Table 1) composed of 10.7% (−)-α-pinene, 0.4% (+)-α-pinene, 13.7% (−)-β-pinene, 7.3% myrcene, 1.5% 3-carene, 0.1% α-phellandrene, 63.7% (+)-β-phellandrene, 0.3% γ-terpinene, and 2.4% terpinolene (experiments 2 and 3) (Table 1). These proportions represent an average of those found in subalpine firs, *Abies lasiocarpa*, and Engelmann spruce, *Picea engelmannii*. Experiment 1 was run July 7–28, 1999 and had 24 replicates of five traps per replicate, with nine replicates set up in the Gorman Bros. Ltd. mill yard in Westbank, British Columbia, and 15 in the Weyerhaeuser Canada Ltd. mill yard in Okanagan Falls, British Columbia. Experiment 2 was run June 23–August 11, 1999 and had 10 replicates of five traps per replicate set up in a recently thinned white pine stand north of Thessalon, Ontario. The surrounding forest was predominately jack pine, *Pinus banksiana*. Experiment 3 was run July 19–August 14, 1999 and had eight replicates of five traps per replicate in the Slocan Forest Products Ltd., Tackama Division mill yard in Ft. Nelson, British Columbia. Experiment 4 was run June 29–July 31, 1999 and had 20 replicates with 10 each in Ainsworth Forest Products Ltd. mill yards in 100-Mile House and Chasm, British Columbia.

Experiments 1, 3, and 4 used 12-unit multiple-funnel traps (Lindgren, 1983) deployed in randomized complete blocks with traps ≥15 m apart. A small block of Vapona No-Pest Strip (Green Cross, Fisons Horticulture Inc., Mississauga, Ontario) was placed in each collecting cup to minimize predation and cannibalism. Traps were hung from aluminum poles such that the top funnel was ca. 1.5 m above ground. Experiment 2 used cross-vane traps with collection bins containing soapy water, deployed as above (de Groot and Nott, 2001).

The treatments for experiments 1–3 were: (1) unbaited control, (2) host blend alone, (3) host blend and pheromone blend 1, (4) host blend and pheromone blend 2, and (5) host blend and both pheromone blends. Treatments for experiment 4 were: (1) unbaited control, (2) pheromone blend 1, (3) pheromone blend 2, and (4)

both pheromone blends. Release devices and rates for all compounds are given in Table 1.

Captured beetles were collected weekly and frozen until they could be identified and sexed. *Monochamus* spp. were identified and sexed by using elytral, antennal, and sternite characters (Linsley and Chemsak, 1984). Voucher specimens for all species reported have been deposited at the Pacific Forestry Centre, Canadian Forest Service, Victoria, British Columbia.

Data for each sex were transformed by $\log_{10}(x + 1)$ to correct for nonnormality and heteroscedasticity (Zar, 1984), and analyzed by ANOVA (GLM) and the Ryan-Einot-Gabriel-Welsch (REGW) multiple-range test (Day and Quinn, 1989) with SAS Institute Inc. software (SAS Institute Inc., 1988). In all cases $\alpha = 0.05$.

RESULTS

As shown in a representative example from a female *M. scutellatus* antenna (Figure 1), all nine pheromones were detected by the antennae of both male and female *M. scutellatus, M. clamator*, and *M. obtusus*, with no differences by species or sex in the level of response.

In experiment 1, one or both sexes of *M. clamator* and *M. obtusus* were captured in higher numbers in traps baited with the host blend plus pheromone blend 1 than in traps baited with the host blend alone (Figure 2). Fewer *M. obtusus* of both sexes were captured in traps baited with the host blend plus both bark beetle pheromone blends. In no case were there significantly more beetles of either sex captured in traps baited with the host blend plus pheromone blend 2 than in either unbaited traps or traps baited with the host blend alone. Only male *M. obtusus* were more attracted to traps baited with the host blend than to the unbaited control traps.

In experiment 2, both sexes of *M. scutellatus* and *M. notatus* were captured in higher numbers in traps baited with the host blend plus pheromone blend 1. Both sexes of *M. scutellatus* and female *M. notatus* were captured in higher numbers in traps baited with the host blend plus both pheromone blends than in other traps (Figure 2). Similarly, both sexes of *M. scutellatus* and female *M. notatus* were captured in higher numbers in traps baited with the host blend plus pheromone blend 2 or the host blend alone than in unbaited traps. In experiment 3, both sexes of *M. scutellatus* were caught in higher numbers in all baited traps than in unbaited control traps.

In experiment 4, male and female *M. clamator* and *M. scutellatus* were captured in higher numbers in traps baited with pheromone blend 1 alone or combined with pheromone blend 2 than in unbaited traps or traps baited with pheromone blend 2 alone (Figure 3).

For experiments 1, 3, and 4 other wood-borer species were counted and sexed if $\geq$50 individuals were caught. Significant responses, all by beetles in the family

TABLE 1. COMPOUNDS AND THEIR SOURCE, CHEMICAL PURITY, RELEASE DEVICES, ENANTIOMERIC COMPOSITION, AND RELEASE CHARACTERISTICS OF SEMIOCHEMICALS TESTED IN FIELD EXPERIMENTS AS ATTRACTANTS FOR *Monochamus* SPP

Blend and compounds	Source[a]	Chemical purity (%)	Release device[b]	Enantiomeric composition (+:−)	Release rate (mg/24 hr)[c]
Pheromone blend 1					
Ipsenol	Phero Tech	98	bubble cap	50:50	0.24
Ipsdienol	Phero Tech	95.4	bubble cap	50:50	0.11
MCH	Phero Tech	98.8	bubble cap	50:50	4.5
Frontalin	Phero Tech	99.9	closed 400-μl Eppendorf tube	50:50	2.6
Pheromone blend 2					
endo-Brevicomin	Phero Tech	99.1	closed 250-μl Eppendorf tube	50:50	0.28
exo-Brevicomin	Phero Tech	99	closed 250-μl Eppendorf tube	50:50	0.28
cis-Verbenol	Phero Tech	92.7 (5% *trans*-)	bubble cap	22:78	0.35
trans-Verbenol	Phero Tech	75 (15% *cis*-)	bubble cap	18:82	1.5
Verbenone	Phero Tech	98	bubble cap	18:82	5
Synthetic host monoterpene blend					
(−)-α-Pinene	Aldrich	98	plastic sleeve	81:19	47.5
(+)-α-Pinene	Aldrich	98	plastic sleeve	91:9	1.8
(−)-β-Pinene	Aldrich	99	plastic sleeve	1:99	77.4
Myrcene	Phero Tech	92.6	plastic sleeve	Not Chiral	88.1

3-Carene	Aldrich	90	plastic sleeve	NA[e]	5.4
(−)-α-Phellandrene	Fluka	59.6	plastic sleeve	NA[e]	15.8
(+)-β-Phellandrene[d]	Liberty Natural Products	70	plastic sleeve	99:1	409.9
γ-Terpinene	Aldrich	97	plastic sleeve	Not Chiral	16.9
Terpinolene	Fluka	92.6	plastic sleeve	Not Chiral	36.3
Host compounds released separately					
α-Pinene	Phero Tech Inc.	>99	plastic sleeve	90-95:5-10	2187
Ethanol	Phero Tech Inc.	95	plastic sleeve	Not Chiral	1200

[a]Phero Tech Inc., 7572 Progress Way, Delta, British Columbia V4G 1E9, Canada; Aldrich Chemical Company, Sigma-Aldrich Canada Ltd., 2149 Winston Park Drive, Oakville, Ontario L6H 6J8, Canada; Fluka, Sigma-Aldrich Canada Ltd., 2149 Winston Park Drive, Oakville, Ontario L6H 6J8, Canada; Liberty Natural Products, 8120 SE Stark Street, Portland, Oregon 97215.

[b]All release devices fom Phero Tech Inc. For the host blend, ethanol and all other compounds were released from separate sleeves. All other compounds were released fom separate devices.

[c]Release rates for ipsenol, ipsdienol, MCH, frontalin, *cis*- and *trans*-verbenol, *endo*- and *exo*-brevicomin, and verbenone were determined at 20–23°C by Phero Tech Inc. Rates for (−)-α-pinene, (+)-α-pinene, (−)-β-pinene, myrcene, 3-carene, (−) α-phellandrene, (−)-β-phellandrene, γ-terpinene, terpinolene, α-pinene, and ethanol were determined at 28–30°C at Simon Fraser University.

[d]Obtained from angelica seed oil (Liberty Natural Products). Enantiomeric determination after the field season revealed almost pure (+) enantiomer, the antipode of naturally occuring β-phellandrene in conifers.

[e]Standards not available. Unable to determine.

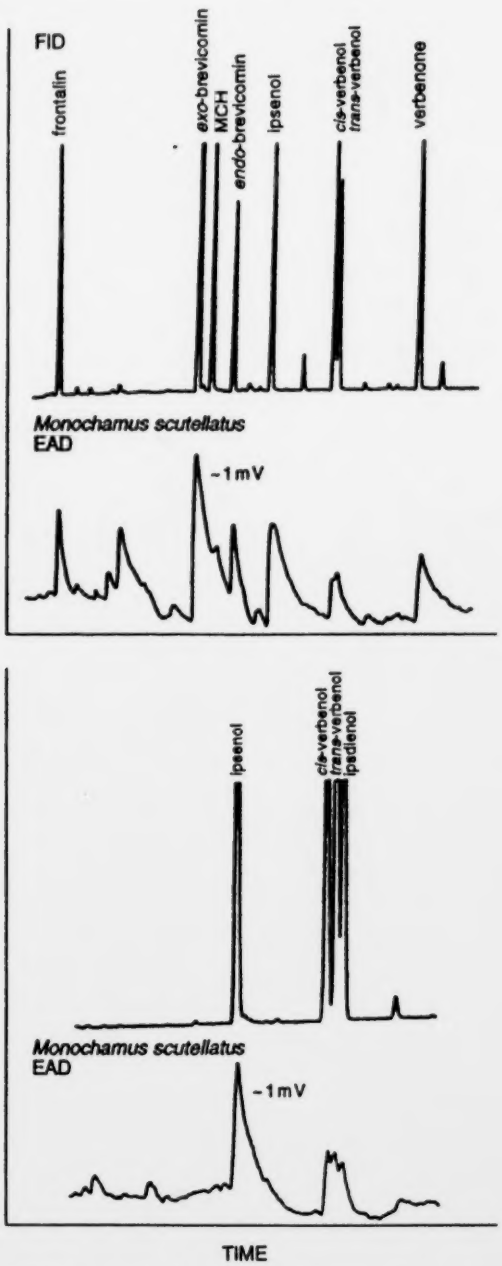

FIG. 1. Responses in GC-EAD analysis of female *M. scatellatas* antenna to nine bark beetle pheromones with a DB-5 column with a temperature program of 60°C (1 min), 10°C/min to 220°C (top), and a DB-5 column with a temperature program of 50°C (1 min), 10°C/min to 90°C, then 4°C/min to 240°C (bottom) to separate ipsdienol from *trans*-verbenol.

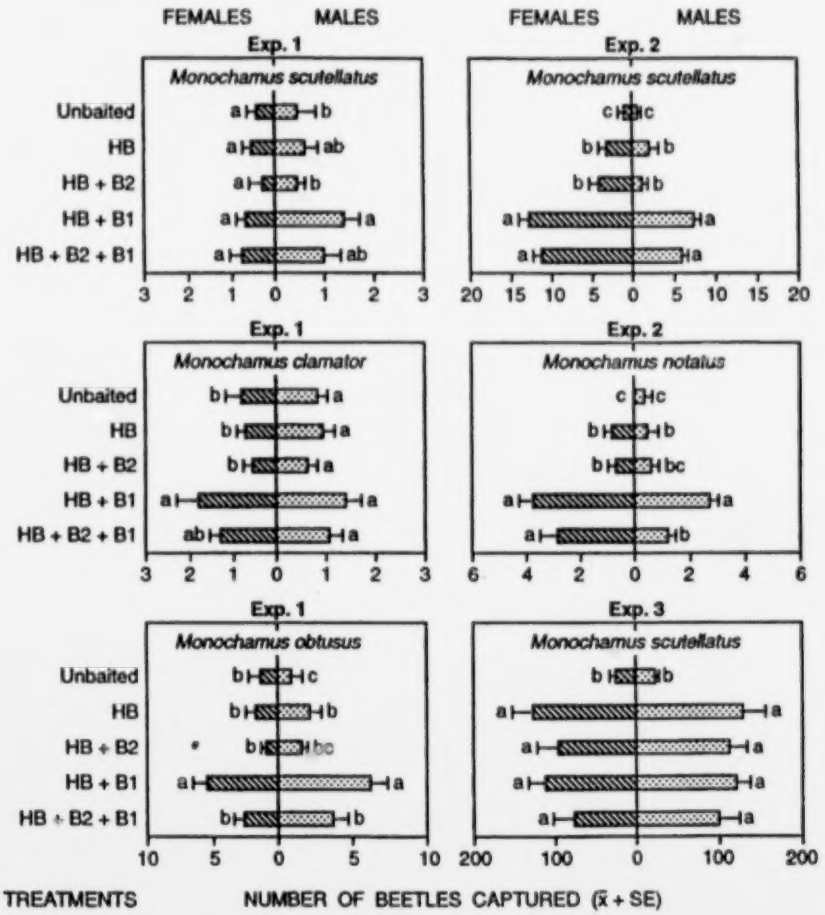

FIG. 2. Catches of four *Monochamus* spp. in experiments 1–3 in unbaited traps or in traps baited with a blend of host compounds alone (HB = host blend) or with pheromone blend 1 (B1), pheromone blend 2 (B2), or both blends together (Table 1). The host blend was composed of ethanol with α-pinene (experiment 1) or a complex blend of monoterpenes (experiments 2 and 3) (Table 1). Means within a species, experiment, and sex followed by the same letter are not significantly different, REGW test, $\alpha = 0.05$.

Buprestidae, were as follows: female *B. subornata* ($N = 89$) in experiment 1 captured in greater numbers in unbaited traps than in traps baited with the host blend and pheromone blend 2, with an intermediate level attracted to the host blend and host blend with pheromone blend 1 or pheromone blends 1 and 2; female *Chalcophora virginiensis* ($N = 158$) in experiment 4 captured in greater numbers in traps baited with pheromone blend 1 alone or with pheromone blend 2 than in other traps; male *Dicerca tenebrica* ($N = 482$) in experiment 4 captured in higher numbers in traps baited with either pheromone blend than in unbaited control traps, with an intermediate level attracted to both pheromone blends combined; female

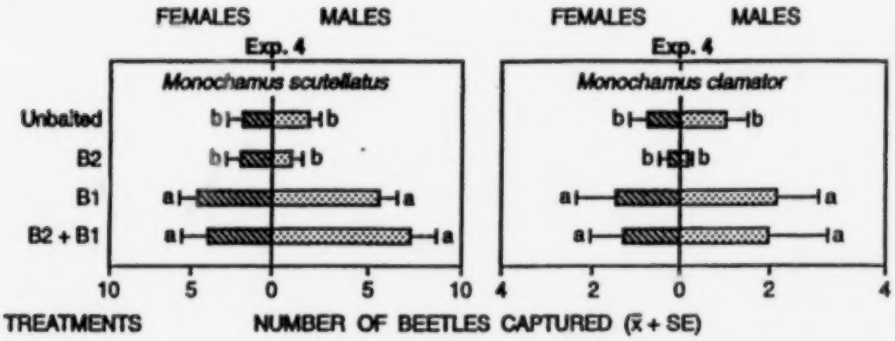

FIG. 3. Catches of *M. scutellatus* and *M. clamator* in experiment 4 in unbaited multiple-funnel traps or in traps baited with pheromone blend 1 (B1), pheromone blend 2 (B2), or both blends together. Means within a species and sex followed by the same letter are not significantly different, REGW test, $\alpha = 0.05$.

D. tenebrica ($N = 1288$) in experiment 4 captured in higher numbers in traps baited with blend 1 than in traps baited with both blends combined and unbaited traps, with an intermediate level attracted to blend 2; and female *Buprestis lyrata* ($N = 46$) in experiment 4 captured in higher numbers in traps baited with phero mone blend 2 than pheromone blend 1, with other treatments intermediate. Despite $\geq$50 beetles being captured, no significantly greater responses to baited over unbaited traps in any experiment were found for the following: *Xylotrechus longitarsus, X. undulatus, Asemum* spp., and *Arhopalus* spp. (all Cermabycidae), *Dicerca tenebrosa, B. nutalli, B. laeviventris, B. maculativentris*, and *Chrysobothris* spp. (all Buprestidae).

DISCUSSION

Our results demonstrate that *M. clamator, M. notatus, M. obtusus*, and *M. scutellatus* can perceive and are attracted by pheromones of sympatric bark beetles in combination with host volatiles. For two species, *M. scutellatus* and *M. clamator*, they also demonstrate that a response can occur to bark beetle pheromones in the absence of host volatiles, supporting the results of Billings and Cameron (1984), but not Billings (1985) for *M. titillator.*

These findings suggest that these *Monochamus* spp. use heterospecific pheromones as kairomones during host selection. The ability to respond to both sympatric bark beetle pheromones and host volatiles would minimize the energy spent in foraging to locate hosts, the exposure to predation or environmental extremes (Dahlsten, 1982), and the opportunity cost of time lost for other biologically important activities (Campbell, 1996) in both the presence and absence of mass-attacking primary and secondary bark beetles.

The occurrence of intraguild predation is well documented in many terrestrial and aquatic communities (Polis et al., 1989). Dodds et al. (2001) recently found that *M. carolinensis* is a facultative, intraguild predator of bark beetle larvae. We hypothesize that *M. clamator, M. notatus, M. obtusus,* and *M. scutellatus* are intraguild predators, and, thus, gain an additional adaptive advantage from being able to orient to bark beetle pheromones. Evolution of a kairomonal response by *Monochamus* spp. to the pheromones of numerous species of sympatric bark beetles would be facilitated by overlapping host ranges and similar larval requirements. The absence of one or both of these may explain why the majority of other wood-borers captured, mainly buprestids, did not respond to either the host or pheromone blends. If *Monochamus* spp. gain a significant adaptive advantage by preying on the larvae of bark beetles, they would inevitably be in competition with entomophagous insects that use the same compounds as kairomones (Borden, 1982).

In Ft. Nelson, population levels during experiment 3 were high, and it is possible that the high numbers of responding beetles obscured responses by *M. scutellatus* to different stimuli. Alternatively, the Ft. Nelson population of *M. scutellatus* may represent a behavioral ecotype that is associated with different bark beetles than those in southern British Columbia or Ontario.

The blends tested contained two antiaggregation pheromones: MCH and verbenone. Positive orientation toward sources of both aggregation and antiaggregation pheromones should be adaptive for *Monochamus* spp., as long as they indicate the presence of a suitable host. However, the lack of a response to pheromone blend 2 alone or combined with the host blend, as well as reduced responses by *M. obtusus* when it was combined with pheromone blend 1 in experiment 1, suggest that one or more of its components, possibly verbenone, could actually be repellent. The production of verbenone by microorganisms (Leufven et al., 1984; Hunt and Borden, 1990) after a host has been overcome by aggressive bark beetles may provide a signal to *Monochamus* spp. of hosts that are no longer acceptable. Verbenone might also be produced by microorganisms associated with larval wood-borers.

Kairomonal responses by *Monochamus* spp. may have practical application in pest management. If further research results in simplified and, thus, inexpensive kairomonal blends composed of both host volatiles and bark beetle pheromones, an improved trap (McIntosh et al., 2001; de Groot and Nott, 2001) baited with a more potent attractive lure might be used effectively in operational monitoring and mass-trapping programs. These in turn could lead to reduced degrade losses and (where pine-wilt disease occurs) curtailment of the spread or infection rate of the pine wood nematode.

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